

BIOLOGY AND HOST-PLANT RELATIONSHIPS OF AN OLIGOPHAGOUS
LEAF MINER *PHYTOMYZA MATRICARIAE* HENDEL (DIPTERA:AGROMYZIDAE)

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The members of this species feed in nature only on representatives of the plant genera *Achillea*, *Chrysanthemum*, *Matricaria* and *Tanacetum* belonging to the tribe *Anthemideae*, family *Compositae*. Natural incidence, mating, adult and larval feeding, oviposition, life cycle and immature stages on *Tanacetum vulgare* L. were observed. Thirty-eight plant species belonging to 17 families were tested for acceptability to gravid females for feeding and oviposition. Comparison of index of acceptability for feeding and oviposition with an index of plant relationship show that only plants closely related phylogenetically to the natural host-plant were acceptable for feeding and oviposition. This ovipositional preference by adult females is probably due to host-specific substances present only in selected plants. Studies on feeding and ovipositional preference by adult females when offered a choice of six acceptable plants show that maximum numbers of feeding punctures were on the plant from which flies were bred. Other preferred plants also served as hosts in nature. Two genera, *Artemisia* and *Helianthus*, though acceptable but not preferred in these studies do not serve as hosts in nature. The larva being a completely internal plant feeder is unable to select a more suitable food plant which might be available in its range. First instar larvae were manually transferred from the natural host-plants in various test plant species. Comparison of the success index for larval development with the index of plant relationship show that some plants widely removed phylogenetically but presumably lacking toxic or inhibitory substances were nutritionally adequate for completion of larval development.

Die zu dieser Art gehörenden Insekten ernähren sich unter natürlichen Verhältnissen nur von Pflanzen der Gattungen *Achillea*, *Chrysanthemum*, *Matricaria* und *Tanacetum* die zu der Familie *Compositae*, Tribus *Anthemideae* gehören. Vorkommen, Paarung, Nahrung der Imagines und der Larven, Eiablage, und Entwicklungsstadien einschliesslich der Larven und Puppen, wurde unter natürlichen Bedingungen an *Tanacetum vulgare* L. beobachtet. Bezüglich ihrer Eignung für Nahrungsaufnahme und Eiablage wurden 38 Pflanzenarten von 17 Familien für ihre Anziehungskraft auf das Trächtige Weibchen untersucht. Ein Vergleich des Indexwertes der Anziehungskraft für Frass und Eiablage mit dem des Verwandtschaftsgrades der Pflanzen zeigt, dass nur solche Pflanzen für Nahrungsaufnahme und Eiablage angenommen werden, die phylogenetisch mit der Wirtspflanze nahe verwandt sind. In Hinsicht auf die Eiablage ist diese Bevorzugung durch das Weibchen wahrscheinlich in wirtspezifischen Substanzen zu suchen, die nur in ausgesuchten Pflanzen vorhanden sind. Wenn eine Wahl von 6 bekömmlichen Pflanzen für Nahrungsaufnahme und Eiablage geboten wurde, zeigte es sich in der folgenden Untersuchung, dass die grösste Anzahl von Einstichen in den Pflanzen gefunden wurde, auf denen die Fliegen vorher herangezogen worden waren. Andere bevorzugte Pflanzen dienen in natürlicher Umgebung auch als Wirte. Zwei Gattungen, *Artemisia* und *Helianthus*, zwar geeignet aber nicht bevorzugt in den Versuchen, dienen in der Natur nicht als Wirtspflanzen. Da die Larve ausschliesslich im Inneren der Pflanze Nahrung sucht, kann sie nicht einen anderen, in der Nähe vorhandenen, besser geeigneten Wirt aussuchen. Larven die sich im ersten Stadium befanden, wurden manuell vom natürlichen Wirt auf die Versuchspflanze übertragen. Ein Vergleich der Erfolgszifferwerte der Larvenentwicklung mit denen des Verwandtschaftsgrades der Pflanze, zeigte, dass einige phylogenetisch nicht sehr nahe Pflanzen nahrungsmässig bekömmlich genug waren, um eine volle Entwicklung der

Larven herbeizuführen. Es ist anzunehmen, dass in diesem Falle toxische oder hemmende Substanzen nicht vorhanden waren.

Most of our knowledge of the biology of agromyzid flies is due to the late Professor E. M. Hering who in 1951 reviewed all existing information and compiled an extensive bibliography on this subject. Numerous other workers have studied the biology of many leaf mining species in detail (Webster and Parks, 1913; Smulyan, 1914; Cohen, 1936; Ahmad and Gupta, 1941; Allen, 1956; Oatman and Michelbacher, 1958, 1959; Tauber and Tauber, 1968).

Phytomyza matricariae Hendel is an oligophagous species whose members feed in nature around Edmonton, Alberta, Canada, only on the representatives of the tribe Anthemideae, family Compositae. The plant species attacked are *Achillea millefolium* Michx. (Fig. 1), *Achillea sibirica* Ledeb. (Fig. 2), *Achillea* sp. (cultivated variety), *Chrysanthemum* sp. (cultivated soft leaf variety), *Matricaria matricarioides* (Less.) Porter (Fig. 3), and *Tanacetum vulgare* L. (Fig. 4). Hering (1957) lists *Achillea*, *Anacyclus*, *Anthemis*, *Cotula* and *Matricaria* as European hosts for the members of this species. However, the identity of flies bred from some of these hosts probably needs confirmation by examination of the male genitalia. Spencer (1969) lists *Tanacetum* also as a European host.

Literature on various aspects of host selection, feeding, and host preference in phytophagous insects has been reviewed by many authors (Lipke and Fraenkel, 1956; Friend, 1958; Thorsteinson, 1960; Kennedy, 1965; Dethier, 1966, 1970; Schoonhoven, 1968).

Verschaffelt (1910) for the first time demonstrated that host selection in *Pieris brassicae* and *P. rapae* is determined by mustard oil glucosides in cruciferous and related plant families. Since then the food ranges of many oligophagous insects have been explained by the botanical distribution of secondary plant chemicals (Fraenkel, 1959). Feeding or token stimuli which evoke special feeding responses in phytophagous insects have been investigated (Thorsteinson, 1953; Sugiyama and Matsumoto, 1959; Nayar and Fraenkel, 1962, 1963; Harris and Mohyuddin, 1965; Keller and Davich, 1965; Stride, 1965) and together with deterrents play an important role in determining the selection of host-plants (Thorsteinson, 1960; Jermy, 1961, 1964). Many recent studies on the host range of oligophagous species have shown that plants not closely related to natural host-plants may be acceptable for normal growth and development (Jermy, 1961, 1966; Hsiao and Fraenkel, 1968). The association between insects and their host-plants has been shown to be the consequence of the interaction of two independently mutating systems (Dethier, 1970), and of the evolutionary coadaptations to chemical interactions between them (Whittaker and Feeny, 1971).

Most research in the field of insect host-plant relationships has been on external plant feeders. Agromyzids having evolved as exclusively internal plant feeders are more closely bound to plants than any group of external feeders and are therefore ideal for the study of insect-food plant relationships. The female agromyzid deposits an egg individually inside the tissue of a selected plant. The emerging larva, unlike that of external plant feeders, is unable to select a more suitable food plant which might be available in its ecological range. The larva either feeds on the plant tissue selected for it by its mother or dies. Although an agromyzid larva is not concerned with the selection of a suitable food plant, it is directly involved with its acceptance. These larvae are therefore most suitable for the study of their potential to use various food plants for their development.

Host-plant relationships in Agromyzidae have been discussed by Hering (1951), Nowakowski (1962), Spencer (1964) and Sehgal (1971). Among Agromyzidae, monophagy and oligophagy are both of common occurrence. Strict monophagy is rare outside of monotypic genera. Extreme polyphagy is also rare; all known polyphagous species are restricted in their range of food plants. Most species therefore feed in nature on related plants.

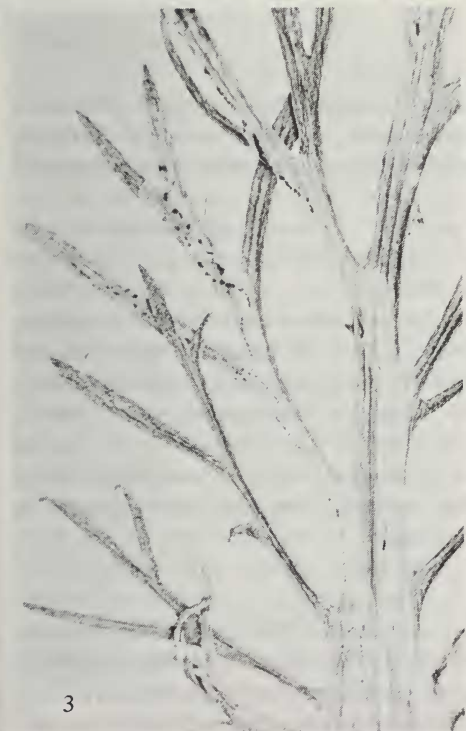
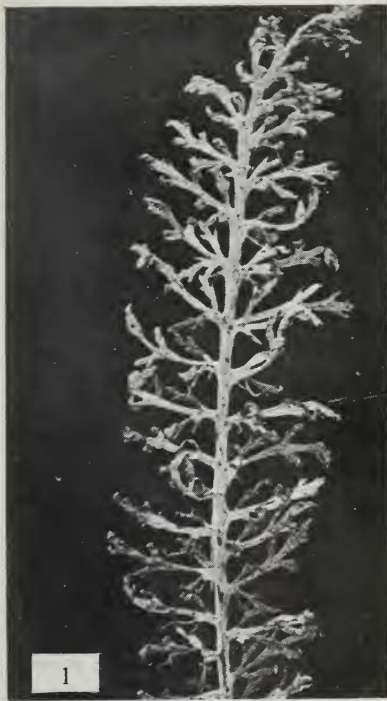


Fig. 1-4. Leaf mines on natural host plants of *Phytomyza matricariae*. 1. *Achillea millefolium* Michx. 2. *Achillea sibirica* Ledeb. 3. *Matricaria matricarioides* (Less.) Porter. 4. *Tanacetum vulgare* L.

MATERIALS AND METHODS

Observations on biology, and host-plant relationships of adult females and larvae were made under laboratory conditions of 70 ± 1 F and 12 hours of daily illumination maintained inside a growth chamber. The flies used in these experiments were bred from *Tanacetum vulgare* L. Both greenhouse and field grown plants were used. Small cuttings from the test plants were kept in Sach's culture solution for flowering plants. By changing the solution it was possible to keep the cuttings healthy during the test period.

Biology of *Phytomyza matricariae* Hendel

Observations on mating, oviposition, feeding habits, and life cycle, were made on *Tanacetum vulgare* L. In order to determine the incubation period, individual leaves were caged with a large population of flies. After six hours the leaves were removed, examined for eggs, and the positions of individual eggs marked. The leaves were then observed at 12 hour intervals. The progress of larval mines was marked with different water soluble colors every 12 hours and the mine examined for moulted mouth hooks, which can be seen inside the mine by transmitted light under a binocular microscope. Duration of larval stadia was estimated from the positions of moulted mouth hooks. The time of moulting during any 12 hour period was estimated by measuring the relative length of leaf mine before and after the position of moulted mouth hooks. This method of recording larval activity has been used by Allen (1956) and Tauber and Tauber (1968). It was thus possible to estimate the duration of larval stadia, length of leaf mine excavated by different instars, and observe the mining habits of the larva. Leaf mines were fixed in 'Formal Acetic Alcohol' (F.A.A.) for microtomy.

Host-plant relationship in adult females

Range of food plants. — Small twigs of various plant species, bearing young leaves, were exposed individually to five gravid females inside a muslin cage, for a period of 24 hours. At the end of the experiment, flies were removed from the cages and the leaves examined for feeding punctures and punctures with eggs.

Feeding and oviposition preference by gravid females. — A circular plastic petri dish 5½ inches in diameter was used as a choice chamber to test the feeding and oviposition preference of adult females. The young leaves of six different plants, grown under greenhouse conditions, were placed around the periphery of the dish equidistant from one another. The petioles of leaves were pulled out through small holes in the periphery of the dish and wrapped with cotton kept moist with distilled water. The plants used in this experiment were *Tanacetum vulgare* L., *Achillea sibirica* Ledeb., *Matricaria matricarioides* (Less.) Porter, *Artemisia* sp., *Chrysanthemum* sp., (cultivated variety) and *Helianthus annuus* L. Five gravid females from a laboratory culture maintained on *Tanacetum vulgare* L. were used in each test after being isolated from their food plant for one hour. They were anesthetized with CO₂ and then introduced at the centre of the petri dish.

Host-plant relationships of the larva

Transfers of larvae from natural host-plants to test plants. — First instar larvae normally less than 24 hours old were used in these experiments. The supply of healthy first instar larvae was from plants in which eggs were laid in the laboratory. Field collected larvae were not used in order to avoid any early parasitization by braconids or chalcidoids.

Only young and tender leaves which are easier to handle than the mature leaves were used in these experiments. A small slit was made in the leaf of a test plant, using fine insect

pins under a binocular microscope. It is normally easier to make the slit near the base of the leaf or near the mid rib, more so on one side of the leaf than the other, depending on the test plant. A first instar larva was then removed by opening its mine on the natural host-plant and transferred with a fine tip of a soft brush into the slit made on the leaf of the test plant. The larva was pushed inside the slit so that it was completely surrounded by the tissue of the test plant. The leaf of the test plant along with a small portion of petiole or twig was then enclosed inside a square plastic petri dish containing moist filter paper in order to prevent any sudden drying of the tissue around the slit. Two small holes were cut in upper corners of the petri dishes and covered with thin muslin cloth to permit transpiration and to prevent excessive condensation. The larva inside the test plant can be observed by transmitted light, moving its mouth hooks in an attempt to eat the new tissue. Leaves of the test plants were checked within a couple of hours of making the transfers. If the larva was still moving its mouth hooks, the transfer was considered successful; if the larva did not show any movement it was assumed to have been injured and the transfer was rejected. With patience and experience with particular test plant, it was possible to make good transfers of larvae, except to *Artemisia* because of the very woolly surface of the leaf. The transferred larva usually ended up inside the fibres on the leaf, rather than inside the leaf tissue.

Observations were made every 12 hours on larval feeding and pupation, if any, during the previous 12 hour period. The pupae obtained were kept individually in small vials containing moist sand, for emergence of adults. The emergence of adults was also checked every 12 hours.

BIOLOGY OF *PHYTOMYZA MATRICARIAE* HENDEL

Natural incidence

The adults of this species appear around Edmonton, Alberta during the first week of June. The leaf mines and larvae start appearing on various host-plants by the second week of June. There are numerous overlapping generations during July, August, and up to mid-September, when numbers start declining. At this time the host-plants also decline in vigor due to shorter days and lower temperatures. Towards the end of September, puparia go into winter diapause.

Mating

Mating was observed in the laboratory and it occurs many times in the life of both sexes, usually on the leaves of the food plant. The mating posture in a superimposed position is typical of other agromyzid flies. Its duration as in other agromyzid flies varies greatly, from ½ hour to approximately 2 hours.

Adult feeding

The flies feed upon plant exudates soon after emergence. The female selects a suitable spot on the leaf tissue, bends the tip of her abdomen vertically downwards, pierces the epidermis and then rotates the tip of her ovipositor within the leaf tissue. She then withdraws her ovipositor, turns around and imbibes the sap exuding from the wound. The puncture thus made is almost conical in shape. This method of feeding among agromyzid flies is of wide occurrence and has been described for many species.

The female spends most of her lifetime making punctures in leaf tissue. These punctures are made both on upper and lower surfaces of the leaf, but are usually more numerous on the upper surface. The males, which are incapable of making such punctures, feed on the sap from punctures made by females or on natural plant exudates and probably also on

nectar of flowers. Pollen grains could not be found in the guts of about 10 field collected males examined for this purpose.

Plants normally survive the injury made by feeding punctures on the leaf, but under severe laboratory infestations they become greatly etiolated and sometimes collapse.

Oviposition

The eggs are laid singly inside the leaf parenchyma in punctures made in a similar way to feeding punctures. The egg punctures, like feeding punctures, were found both on upper and lower surfaces of the leaf, but unlike feeding punctures were usually more common on the lower surface. Feeding punctures always greatly outnumber oviposition punctures. This method of oviposition is general among the leaf mining agromyzid flies and has been described in many species.

Incubation period

The incubation period (Table 1) ranged from 90-102 hours, with an average of approximately 91 hours or 3.8 days. The egg, originally translucent, becomes opaque white within the first 24 hours. The cephalopharyngeal skeleton appears as a darkly sclerotized structure at the end of 72 hours. At this time the embryo is almost fully developed and the mouth hooks can sometimes be seen to move horizontally.

Table 1. Duration of life history of *Phytomyza matricariae* Hendel on its natural host-plant *Tanacetum vulgare* L.

Stage	Number of records	Duration in hours	Total average duration (days)
Egg	44	91.0 (90.0-102.0)*	3.8
First instar	20	64.2 (55.0-73.0)	
Second instar	20	45.0 (40.0-51.5)	
Third instar	20	56.4 (44.0-65.0)	
TOTAL larval	20	165.6 (144.0-180.0)	6.9
Pupal stage	15	13.7 (13.0-14.5) (days)	13.7
TOTAL life cycle			24.4

*The values of 40 observations were 90.0 hours and four 102.0 hours.

Larval activity

The average duration of first, second, and third instars (Table 1) was 64.2, 45.0 and 56.4 hours respectively. The total larval period was 165.6 hours or 6.9 days on an average.

From hatching to shortly before pupation, the larva is completely endophagous. This results in the excavation of a linear leaf mine. The mine starts from the upper or lower surface of the leaf depending upon the site of oviposition and may terminate on either surface, when the larva leaves by cutting a small crescent shaped slit. The larva then falls to the ground and pupates. The larva like most other agromyzid larvae (Hering, 1951)

seems unable to re-enter the leaf once it is removed from it. The ability of the larvae of '*Liriomyza pusilla* Meigen' (Tilden, 1950) and at least some members of the *Agromyza rufipes* group (Nowakowski, 1964; Griffiths, verbal communication) to re-enter the leaf seems very unusual.

The mouth hooks can be seen cutting through the leaf tissue in a lateral and semicircular motion. The larvae, like those of other agromyzids (Hering, 1951), mine the leaf while lying on their sides and they alternate from one side to the other. The frass is deposited in discrete granules along the sides of the mine alternately as the larva turns from side to side. Many larvae may start mining the same leaf simultaneously resulting in numerous mines crossing each other, however, every mine remains distinct and contains only one miner. The larvae normally feed only on the leaf tissue, but in heavy infestations also migrate to the petiole or mine under the epidermis of the stem.

Transverse sections of the mined leaves (Fig. 5, 6) show that larvae feed indiscriminately on the palisade and spongy mesenchymatous tissue between the two epidermal layers of the leaf. The larvae only consume the entire tissue between upper and lower epidermis when this is very heavily infested. Thus the leaf mine is normally more visible from one side of the leaf. The larvae are capable of crossing the leaf veins but the vascular bundles are not consumed, as also reported in some other agromyzid species (Trehan and Sehgal, 1963; Tauber and Tauber, 1968).

The lengths of mines excavated by first, second and third instar are given in Table 2. The total length of 142.0 mm is much shorter than 273.0 mm for "*Phytomyza lanati* Spencer" (Tauber and Tauber, 1968). Although the duration of the third larval instar is approximately the same as that of the first instar, the major portion of the mining activity was done by the third instar.

Table 2. Lengths of leaf mines excavated by different larval instars of *Phytomyza matrixariae* Hendel in *Tanacetum vulgare* L.

Stage of larva	Length of leaf mine in mm (each 19 observations)	
	Range	Average
First instar	8.0– 18.4	13.5
Second instar	13.4– 42.5	29.1
Third instar	71.2–127.0	99.4
TOTAL larval life	110.0–177.0	142.0

Pupation

The mature larva when ready to pupate leaves the leaf mine and falls to the ground, where it seeks a suitable site for pupation. Often the larva remains sticking to the exit slit in the mine and there forms the puparium. Duration of the puparium averages 13.7 days but varies considerably. The pupae from the fall generation undergo winter diapause.

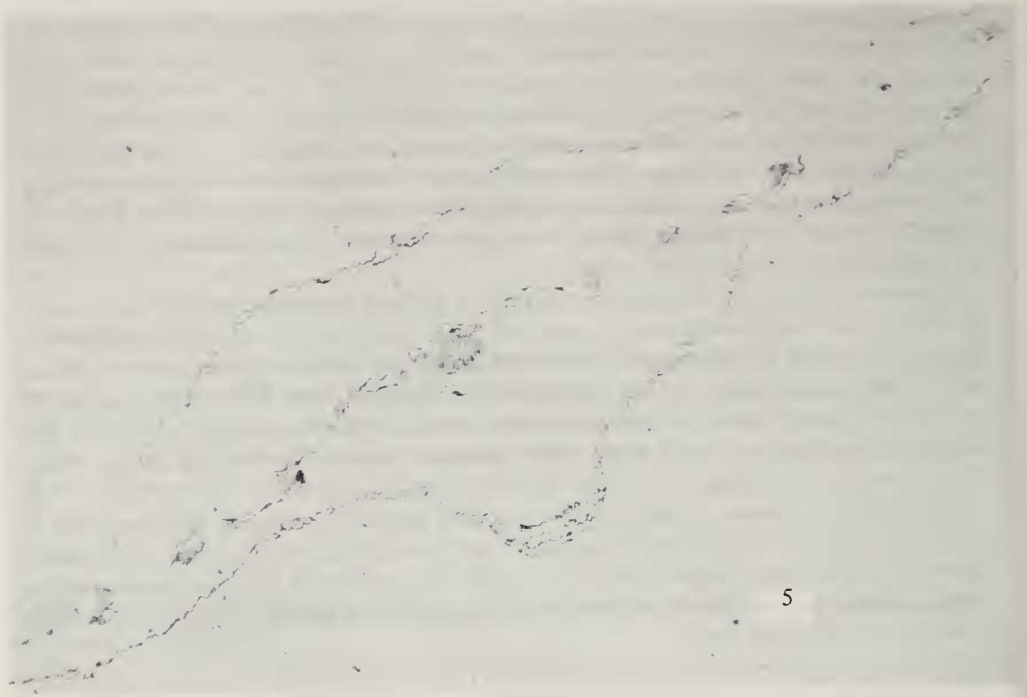


Fig. 5-6. Transverse sections of leaf mines of *Phytomyza matricariae*. 5. leaf mine on *Achillea sibirica* Ledeb. 6. leaf mine on *Matricaria matricarioides* (Less.) Porter.

DESCRIPTION OF THE IMMATURE STAGES

Egg

The egg (Fig. 7) when freshly laid is translucent white, smooth, elongate, ovo-cylindrical, slightly broader at the posterior end, and with a small, almost indistinguishable micropyle at the anterior end. The eggs of the members of the *Phytomyza syngenesiae* group have a similar micropyle (see Smulyan, 1914, '*Phytomyza chrysanthemi* Kowarz' and Cohen, 1936, '*Phytomyza atricornis* Meigen'). The egg dimensions are given in Table 3.

Table 3. The dimensions in mm of egg, larva, cephalopharyngeal skeleton*, and puparium of *Phytomyza matricariae* Hendel. All measurements based on 10 observations.

Stage	Length average (range)	Width average (range)
Egg	0.293 (0.283–0.316)	0.129 (0.100–0.141)
First instar larva	0.412 (0.300–0.550)	0.152 (0.116–0.208)
Cephalopharyngeal skeleton	0.121 (0.116–0.125)	
Second instar larva	0.732 (0.592–0.825)	0.243 (0.208–0.300)
Cephalopharyngeal skeleton	0.220 (0.216–0.233)	
Third instar larva	2.395 (2.125–2.625)	0.667 (0.625–0.750)
Cephalopharyngeal skeleton	0.316 (0.308–0.316)	
Puparium	1.810 (1.675–1.950)	0.852 (0.800–0.925)

* includes mouth hooks, labial sclerite and paired paraclypeal phragma.

Larva

There are three larval instars which can be easily recognised by the sizes of their cephalopharyngeal skeletons (Table 3). The first instar larva when freshly hatched is translucent white, but soon becomes greenish due to the ingested leaf tissue. The second and third instar larvae are yellowish green in colour. The first instar larva is metapneustic, while the second and third instar larvae are amphipneustic. The anterior spiracles (Fig. 8) of the mature third instar larva have 7-9 small oval bulbs, while the posterior ones (Fig. 9) have 19-21 small oval bulbs. De Meijere (1926) illustrated the anterior and posterior spiracles in the European members of this species bred from *Matricaria chamomilla* L. He reported about 12 bulbs on the anterior and 18 bulbs on the posterior spiracles. The head (Fig. 10) bears two small longitudinal sclerites just above the mouth hooks, small but conspicuous maxillary palps, a pair of small antennae and numerous sense papillae. The muscle scars on the intersegmental membrane (Fig. 11) are small, oval and transversely elongated. The tubercle bands (Fig. 11) consist of small conical processes irregularly scattered along the intersegmental membrane. The tubercle bands as in other agromyzid larvae (Allen, 1957) are best developed along lateral portions of intersegmental membrane.

The cephalopharyngeal skeletons of the first, second, and third instar are illustrated in Fig. 12-14. They consist of paired mouth hooks or mandibles, labial sclerite, and paired paraclypeal phragma. The mouth hooks in the first instar larva are small, simple and sickle

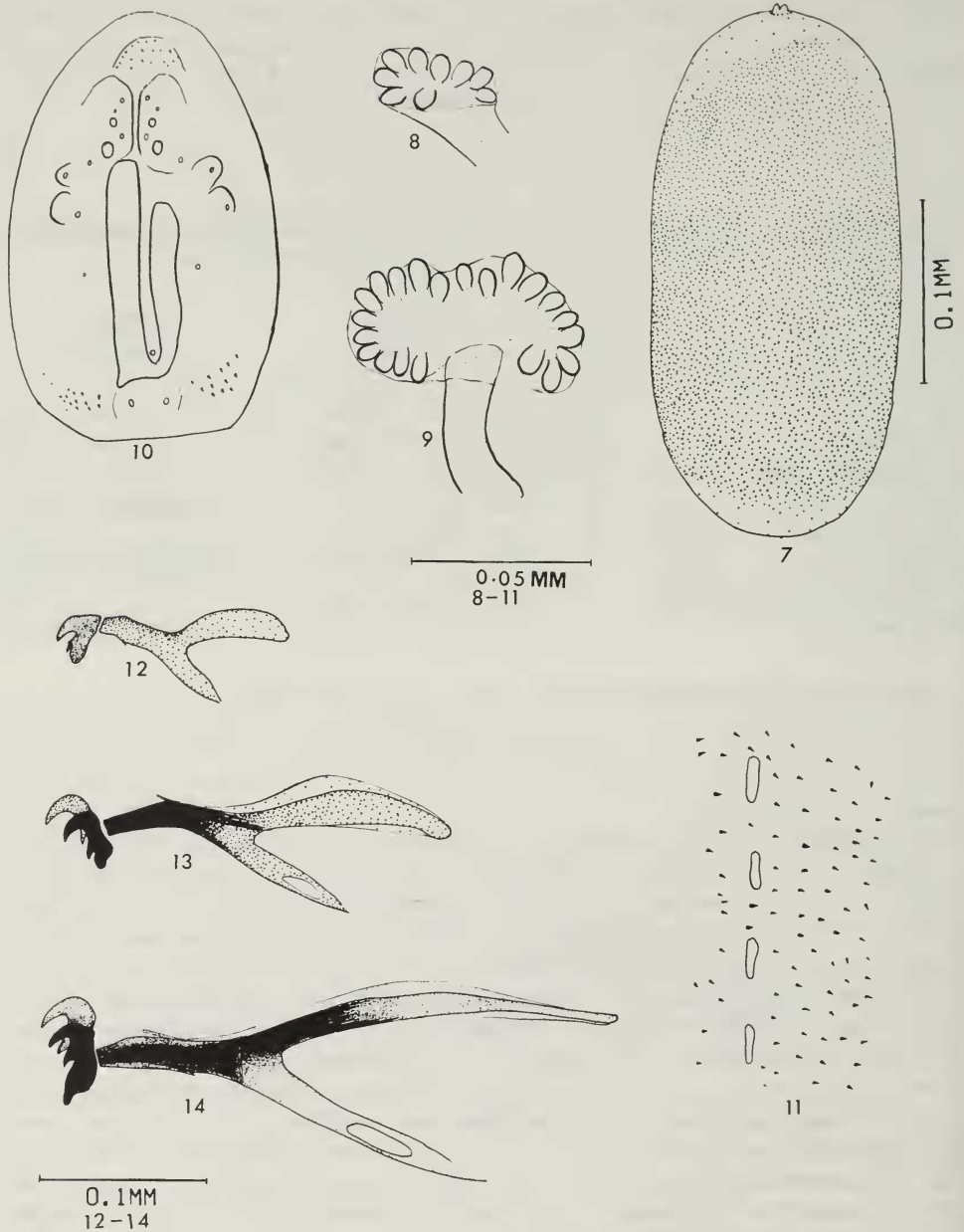


Fig. 7-14. *Phytomyza matricariae*. 7. egg. 8. anterior spiracle. 9. posterior spiracles. 10. facial mask of third instar larva. 11. muscle scars and tubercle band from a lateral portion of first abdominal segment of larva. 12. cephalopharyngeal skeleton of first instar larva. 13. cephalopharyngeal skeleton of second instar larva. 14. cephalopharyngeal skeleton of third instar larva.

shaped; while in second and third instars they are well developed with two teeth each, alternating with one another. The right mouth hook is higher than the left and both mouth hooks are joined at the base (Fig. 10). Labial sclerite and paraclypeal phragma are smaller in first and second instars, but are well differentiated in the third instar. The dorsal process of the paraclypeal phragma consists of a long, single, slender and darkly sclerotized arm; the ventral arm is short, lightly sclerotized, and has a conspicuous foramen towards its posterior end.

Puparium

The puparium dimensions are given in Table 3; it is conspicuously segmented and shining black in colour.

The hardening of the third larval skin is due to the deposition of the calcospherites (Frick, 1952; Allen, 1957) so that it can be softened by treatment with dilute hydrochloric acid and can be cut open for detailed examination. Although the puparium preserves the external morphology of the third instar, this is best studied in the larva itself.

HOST-PLANT RELATIONSHIPS OF ADULT FEMALES

The ovipositing female comes across numerous other plants besides those normally attacked in nature. In order to test the specificity of feeding and oviposition a selection of a wide range of plants was exposed to a batch of five gravid females, for a period of 24 hours. Plants used in this study included some common plants, which the female would encounter in the field, as well as some plants which are known for certain secondary substances like alkaloids, glycosides, etc. A total of 38 plant species belonging to 17 families were tested for feeding and oviposition. Feeding and oviposition preference of females when offered a choice of acceptable plants was also studied. Degree of phylogenetic relationship of the test plant to the natural host-plant was compared with the index of acceptability for feeding and oviposition.

Index of plant relationship

Botanical relationship of the test plant species, used in experiments on feeding and oviposition by adult females and transfers of larvae, to one of the natural food plants of *P. matricariae* was examined.

The phylogenetic relationships between plant families and orders is still a matter of controversy. Most plant classifications fall into two groups depending on the supposed nature of primitive angiosperm flowers (Davis and Heywood, 1965). One system is based on the assumption that the earliest angiosperms were wind-pollinated and that the monocotyledons and dicotyledons have arisen independently from hypothetical gymnosperms. According to the second system dicotyledons and monocotyledons were both derived from primitive angiosperms which were insect-pollinated. The second system has the support of most recent botanists (Eames, 1961; Hutchinson, 1964; Takhtajan, 1969). Hutchinson (1964) has maintained a basic division of dicotyledons into woody "Lignosae" and herbaceous "Herbaceae", a system which allegedly leads to the wide separation of certain plant families which otherwise seem closely related in the structure of their flowers. The arrangement of plant families used in this study is after Takhtajan (1969), which is considered to reflect more closely the phylogenetic relationships between plant families. An index of plant relationship from 1 to 10 was used as follows:

Relationship of the test plant species to natural host-plant	Index of plant relationship
1. Same species	10

2. Same genus	9
3. Same tribe (Anthemideae)	8
4. Same family (Compositae)	7
5. Same order (Asterales)	6
6. Same superorder (Asteranae)	5
7. Same subclass (Asteridae)	4
8. Same class (Dicotyledoneae)	3
9. Same division (Angiospermae)	2
10. Same phylum (Tracheophyta)	1

Acceptability index for feeding and oviposition

Acceptability index (A. I.) of a test plant for feeding and oviposition relative to that of the natural food plant from which flies were obtained was calculated for comparison with the index of plant relationship. In experiments with feeding and oviposition studies, females used were obtained from the natural host-plant *Tanacetum vulgare* L. Data given in Tables 4 and 5 were used to calculate the acceptability index. In order to give a theoretical maximum value of 1 to the acceptability index, the sum of the components was divided by 2; thus:

$$A. I. = \frac{1}{2} \left(\frac{\text{Feeding punctures}}{\text{Feeding punctures in } T. \text{ vulgare}} + \frac{\text{Oviposition punctures}}{\text{Oviposition punctures in } T. \text{ vulgare}} \right)$$

Range of food plants

Data on the acceptability of plants for feeding and oviposition by gravid females is summarized in Table 4. Indices of plant relationship and of acceptability for feeding, and oviposition are given for each plant species. Of the 38 plant species tested only seven belonging to the family Compositae tribes Anthemideae and Heliantheae were acceptable both for feeding and oviposition. Among these *Artemisia*, *Helianthus* and *Zinnia* were not found attacked in nature. The acceptability index for feeding and oviposition based on the data in Tables 4 and 5 is plotted against the index of plant relationship in Fig. 15. Indices of acceptability were very low for most species of test plants, but high for indices of plant relationship of 8 or over.

Feeding and oviposition preference by gravid females

The preference of gravid females for feeding and oviposition when offered a choice of six acceptable plants was examined. The plants used in this study were *Achillea sibirica* Ledeb., *Artemisia* sp., *Chrysanthemum* sp., *Helianthus annuus* L., *Matricaria matricarioides* (Less.) Porter and *Tanacetum vulgare* L. belonging to the family Compositae. Results of this experiment are summarized in Table 5.

The number of feeding punctures on *Tanacetum* was significantly higher than on other plants tested. The numbers of feeding punctures on *Chrysanthemum*, *Achillea*, *Matricaria* and *Helianthus* were not significantly different from each other, but were significantly lower than on *Tanacetum*. The numbers of punctures with an egg on *Tanacetum*, *Chrysanthemum*, *Achillea* and *Matricaria* were not significantly different from each other, but were significantly higher than on *Helianthus* and *Artemisia*. No relationship was found between the numbers of oviposition punctures and the numbers of feeding punctures.

Feeding preferences by freshly emerged females

Feeding preference by freshly emerged females, which had not been exposed to any food plant, was examined in a similar experiment the results of which are summarized in Table 6. The only difference from Table 5 is that the numbers of feeding punctures on *Achillea*, *Matricaria* and *Chrysanthemum* were significantly higher than on *Helianthus* and *Artemisia*.

Table 4. Feeding and oviposition by females of *Phytomyza matricariae* Hendel on various plant species.

Test plant	Number of punctures	Number of punctures with an egg	Index of accepta- bility	Index of plant relationship
PTERIDOPHYTA				
Polypodiaceae				
<i>Nephrolepis</i>	2	0	0.002	1
ANGIOSPERMAE-DICOTYLEDONEAE				
Ranunculaceae				
<i>Aquilegia</i> sp. (cultivated)	16	0	0.018	3
<i>Clematis verticillaris</i> DC	12	0	0.013	3
<i>Delphinium</i> sp. (cultivated)	0	0	0.000	3
Papaveraceae				
<i>Papaver</i> sp. (cultivated)	11	0	0.012	3
Chenopodiaceae				
<i>Chenopodium</i> sp.	5	0	0.005	3
Cucurbitaceae				
<i>Cucumis</i> sp.	11	0	0.012	3
Cruciferae				
<i>Brassica khaber</i> (DC.) Wheeler	3	0	0.003	3
<i>Thlaspi arvense</i> L.	22	0	0.024	3
Rosaceae				
<i>Potentilla</i> sp.	0	0	0.000	3
Leguminosae				
<i>Caragana arborescens</i> Lam.	3	0	0.003	3
<i>Lathyrus odoratus</i> L.	0	0	0.000	3
<i>Lupinus</i> sp. (cultivated)	0	0	0.000	3
<i>Pisum sativum</i> L.	32	0	0.036	3
<i>Vicia americana</i> Muhl.	0	0	0.000	3
Tropaeolaceae				
<i>Tropaeolum</i> sp. (cultivated)	3	0	0.003	3
Solanaceae				
<i>Lycopersicon esculentum</i> L.	3	0	0.003	4
<i>Nicotiana tabacum</i> L.	4	0	0.004	4
<i>Solanum tuberosum</i> L.	3	0	0.003	4
Scrophulariaceae				
<i>Antirrhinum</i> sp. (cultivated)	0	0	0.000	4
Labiatae				
<i>Galeopsis tetrahit</i> L.	5	0	0.005	4
Campanulaceae				
<i>Campanula</i> sp. (cultivated)	0	0	0.000	5
Compositae				
<i>Achillea sibirica</i> Ledeb.	567	28	1.039	8
<i>Artemisia</i> sp.	227	10	0.398	8
<i>Aster ciliolatus</i> Lindl.	10	0	0.011	7

Table 4 (continued)

Test plant	Number of feeding punctures	Number of punctures with an egg	Index of acceptability	Index of plant relationship
<i>Chrysanthemum</i> sp. (cultivated)	467	34	1.012	8
<i>Helianthus annuus</i> L.	292	19	0.600	7
<i>Matricaria matricarioides</i> (Less.) Porter	441	30	0.926	8
<i>Senecio vulgaris</i> L.	54	0	0.060	7
<i>Solidago</i> sp.	12	0	0.013	7
<i>Sonchus uliginosus</i> Bieb.	4	0	0.004	7
<i>Tanacetum vulgare</i> L.	443	35	1.000	10
<i>Taraxacum officinale</i> Weber	124	4	0.139	7
<i>Zinnia</i> sp. (cultivated)	44	3	0.092	7
ANGIOSPERMAE-MONOCOTYLEDONAE				
Liliaceae				
<i>Allium cepa</i> L.	1	0	0.001	2
<i>Smilacina stellata</i> (L.) Desf.	0	0	0.000	2
Gramineae				
<i>Hordeum vulgare</i> L.	7	0	0.007	2
Typhaceae				
<i>Typha latifolia</i> L.	0	0	0.000	2

Table 5. Feeding and oviposition preferences of female *Phytomyza matricariae* Hendel from a culture raised on *T. vulgare*.

Test plant	Average* number of feeding punctures	Average number of punctures with an egg	Index of success	Index of plant relationship
<i>Tanacetum vulgare</i>	519.5 a**	11.8 a'	1.000	10
<i>Chrysanthemum</i> sp.	200.5 b	13.3 a'	0.756	8
<i>Achillea sibirica</i>	181.6 b c	10.5 a'	0.614	8
<i>Matricaria matricarioides</i>	161.0 b c	15.0 a'	0.790	8
<i>Helianthus annuus</i>	58.5 b c	2.3 b'	0.153	7
<i>Artemisia</i> sp.	36.8 c	1.6 b'	0.102	8

* Averages are based on six replicates.

** Treatments which are not significantly different from each other have the same letter opposite; as calculated by Duncan's multiple range significance level test.

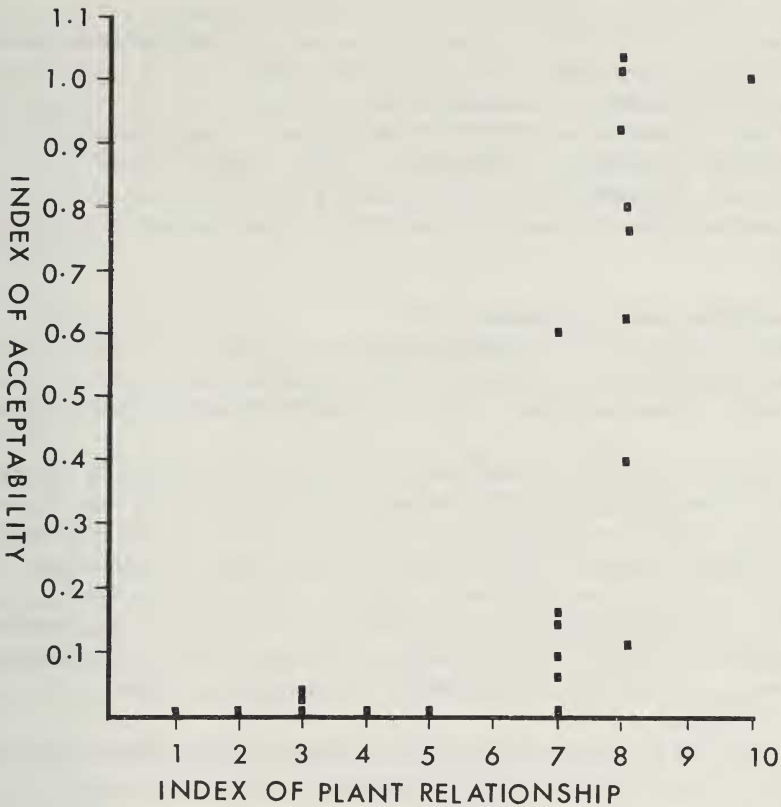


Fig. 15. Graph showing the index of acceptability of test plant for feeding and oviposition, and the index of plant relationship.

Table 6. Feeding preferences of freshly emerged (<24 hours) females of *Phytomyza matricariae* Hendel from *T. vulgare*.

Test plant	Average number of feeding punctures*
<i>Tanacetum vulgare</i>	250.8 a**
<i>Achillea sibirica</i>	174.6 b
<i>Matricaria matricarioides</i>	139.5 b
<i>Chrysanthemum</i> sp.	128.6 b
<i>Helianthus annuus</i>	28.3 c
<i>Artemisia</i> sp.	14.3 c

* Based on six tests.

** Treatments which are not significantly different from each other have the same letter opposite; as calculated by Duncan's multiple range significance level test.

HOST-PLANT RELATIONSHIPS OF LARVAE

In nature the larvae feed only on the plants accepted for oviposition by the female. Being completely internal plant feeders, they cannot select a more suitable food plant which might be available in its geographical range. In order to test the ability of larvae to use different plants as food which may be available in their geographical range, the first instar larvae obtained from the natural food plant were transferred into the tissue of the test plant. An index of success for larval development based on larval feeding, pupation, and emergence of imago was calculated for comparison with the index of plant relationship.

Index of success for larval development

An index of success (S. I.) for larval development was calculated from results obtained in the transfers of larvae from natural host-plant into recipient plant species, for comparison with the index of plant relationship. This calculation was based on three components as follows:

1. *Duration of larval survival in recipient plant.* — This was expressed in half days; the 12 hours immediately preceding the finding of a non-feeding larva was included since observations showed that the average survival time after the cessation of feeding was about 12 hours. Studies on the life history as summarized in Table 1 show that the average duration of a larval stage in *P. matricariae* on *T. vulgare* is 6.9 days. The first instar larvae used in transfer experiments were about 1 day old. Therefore under normal conditions the remainder of larval feeding time should average 5.9 days. Success in larval feeding was expressed as the ratio of the duration of feeding of larva on test plant to 5.9 days.
2. *Pupation.* — This is considered as successful termination of larval development. Success was expressed as the proportion of the transferred larvae pupating successfully on the test plant.
3. *Emergence.* — In most plants the larvae which pupated also emerged as adult flies. The emergence was given one-fourth as much weight as pupation in calculation of success index, that is, it was expressed as one quarter of the proportion of transferred larvae which yielded adult flies.

In order to give a theoretical maximum value of 1 to the Success Index (S. I.) the sum of these components was divided by 2.25; thus:

$$S. I. = \frac{1}{2.25} \left(\frac{\text{Survival time (days)}}{5.9} + \frac{\text{Pupations}}{\text{Transfers}} + \frac{\text{Emergences}}{4 \times \text{Transfers}} \right)$$

Transfers of larvae from natural host-plant to test plant

The number of larvae transferred individually from the natural host-plant to inside the tissue of recipient plant species was 20, except in two species where it was 10. Results of the transfers of larvae are summarized in Tables 7 and 8. Values for the success index and the index of plant relationship are also given graphically in Fig. 16.

Among Pteridophyta, only the greenhouse fern *Nephrolepis* sp. tested for transfers of larvae from *Tanacetum*, could not be used by larvae as food for completing their development indicating the plant to be toxic or otherwise unacceptable.

Among dicotyledons, 28 plants belonging to 10 plant families were tested for transfers of larvae from *Tanacetum* (Table 7) and *Achillea* (Table 8). One larva at least completed its development on 16 plant species belonging to 5 families. Leaf mines formed after transfer of larvae from *Tanacetum* into four of the test plants are shown in Fig. 17-20.

Table 7. Results of transfers of larvae of *Phytomyza matricariae* Hendel from *Tanacetum vulgare* L. to other plant species. 20 transfers except where indicated. Note that transfers to *T. vulgare* represent a control.

Recipient species	Duration of larval feeding in test plant (days)	Number of larvae pupated (**emerged)	Index of success	Index of plant relationship
PTERIDOPHYTA				
Polypodiaceae				
<i>Nephrolepis</i> sp. (cultivated)	*0.25 ± 0.0 (0.5–0.5)	0	0.018	1
ANGIOSPERMAE-DICOTYLEDONEAE				
Ranunculaceae				
<i>Aquilegia</i> sp. (cultivated)	*2.57 ± 3.0 (0.5–9.0)	3	0.276	3
Caryophyllaceae				
<i>Silene noctiflora</i> L.	*1.07 ± 0.3 (1.0–2.0)	0	0.080	3
Chenopodiaceae				
<i>Chenopodium album</i> L.	*0.97 ± 0.5 (0.5–2.0)	0	0.072	3
Cruciferae				
<i>Brassica khaber</i> (DC.)	*2.47 ± 2.0 (1.0–7.5)	2	0.241	3
<i>Thlaspi arvense</i> L.	*1.80 ± 0.8 (1.0–4.0)	0	0.135	3
Rosaceae				
<i>Potentilla</i> sp.	*0.67 ± 0.4 (0.5–2.0)	0	0.050	3
Leguminosae				
<i>Lathyrus odoratus</i> L.	*1.55 ± 1.0 (0.5–4.0)	0	0.116	3
<i>Lupinus</i> sp.	*1.72 ± 0.9 (1.0–4.5)	0	0.129	3
<i>Melilotus officinalis</i> (L.) Lam.	*3.07 ± 2.6 (1.0–9.0)	2 (1)	0.280	3
<i>Pisum sativum</i> L.	*4.47 ± 1.3 (2.0–6.5)	12	0.669	3
Umbellifereae				
<i>Apium</i> sp.	*0.35 ± 0.2 (0.5–1.5)	0	0.026	3
Solanaceae				
<i>Nicotiana tabacum</i> L.	*0.25 ± 0.1 (0.2–1.0)	0	0.018	4

Table 7 (continued)

Recipient species	Duration of larval feeding in test plant (days)	Number of larvae pupated (**emerged)	Index of success	Index of plant relationship
Labiatae				
<i>Galeopsis tetrahit</i> L.	*3.65 ± 1.9 (1.0-7.0)	10	0.552	4
Compositae				
<i>Achillea sibirica</i> Ledeb. (10 transfers)	*4.65 ± 1.4 (1.0-6.0)	9 (8)	0.594	8
<i>Artemisia</i> sp. (10 transfers)	*0.25 ± 0.0 (0.5-0.5)	0	0.018	8
<i>Chrysanthemum</i> sp. (cultivated)	*4.07 ± 2.8 (1.5-8.5)	6	0.472	8
<i>Dahlia</i> sp. (cultivated)	*2.37 ± 1.8 (1.0-8.0)	2 (1)	0.228	7
<i>Helianthus annuus</i> L.	*2.97 ± 2.3 (0.5-6.0)	10	0.501	7
<i>Matricaria matricarioides</i> (Less.) Porter (10 transfers)	*4.40 ± 1.4 (0.5-5.5)	9	0.580	8
<i>Senecio vulgaris</i> L.	*3.85 ± 2.2 (0.5-7.5)	6 (5)	0.450	7
<i>Sonchus uliginosus</i> Bieb.	*3.02 ± 2.6 (0.5-7.0)	9	0.476	7
<i>Tanacetum vulgare</i> L.	*5.57 ± 1.0 (2.0-7.0)	19	0.966	10
<i>Taraxacum officinale</i> Weber	*2.25 ± 2.3 (0.5-6.0)	4 (3)	0.274	7
ANGIOSPERMAE-MONOCOTYLEDONEAE				
Liliaceae				
<i>Allium cepa</i> L.	*3.95 ± 2.4 (1.0-9.0)	6 (5)	0.458	2
Gramineae				
<i>Hordeum vulgare</i> L.	*2.67 ± 1.7 (1.0-7.0)	3	0.284	2
Typhaceae				
<i>Typha latifolia</i> L.	*0.55 ± 0.2 (0.5-1.0)	0	0.041	2

* mean ± S. D.
(range)

** all emerged unless otherwise indicated.

Table 8. Results of transfers of larvae of *Phytomyza matricariae* Hendel from *Achillea sibirica* Ledeb. to test plants. 20 transfers except where indicated. Note that transfers to *A. sibirica* represent a control.

Recipient species	Duration of larval feeding in test plant (days)	Number of larvae pupated (**emerged)	Index of success	Index of plant relationship
ANGIOSPERMAE-DICOTYLEDONEAE				
Cruciferae				
<i>Brassica oleracea</i> L.	*1.50 ± 0.9 (0.5–5.5)	1	0.140	3
Leguminosae				
<i>Lupinus</i> sp. (cultivated)	*1.45 ± 1.3 (0.5–7.0)	0	0.108	3
<i>Pisum sativum</i> L.	*4.17 ± 1.2 (2.0–6.0)	10	0.591	3
Solanaceae				
<i>Nicotiana tabacum</i> L.	*0.80 ± 0.4 (0.5–2.0)	0	0.060	4
<i>Solanum tuberosum</i> L. (10 transfers)	*0.50 ± 0.4 (0.5–1.5)	0	0.037	4
Compositae				
<i>Achillea sibirica</i> Ledeb.	*4.72 ± 1.6 (1.0–7.5)	15	0.772	10
<i>Solidago</i> sp.	*0.67 ± 0.4 (0.5–2.0)	0	0.050	7
<i>Sonchus arvensis</i> L.	*1.50 ± 1.3 (1.0–6.0)	0	0.112	7
<i>Tanacetum vulgare</i> L. (10 transfers)	*5.05 ± 1.1 (2.5–6.5)	9	0.880	8
<i>Zinnia</i> sp. (cultivated)	*2.72 ± 1.5 (1.0–5.5)	6 (5)	0.365	7

* mean ± S. D.
(range)

** all emerged unless otherwise indicated.

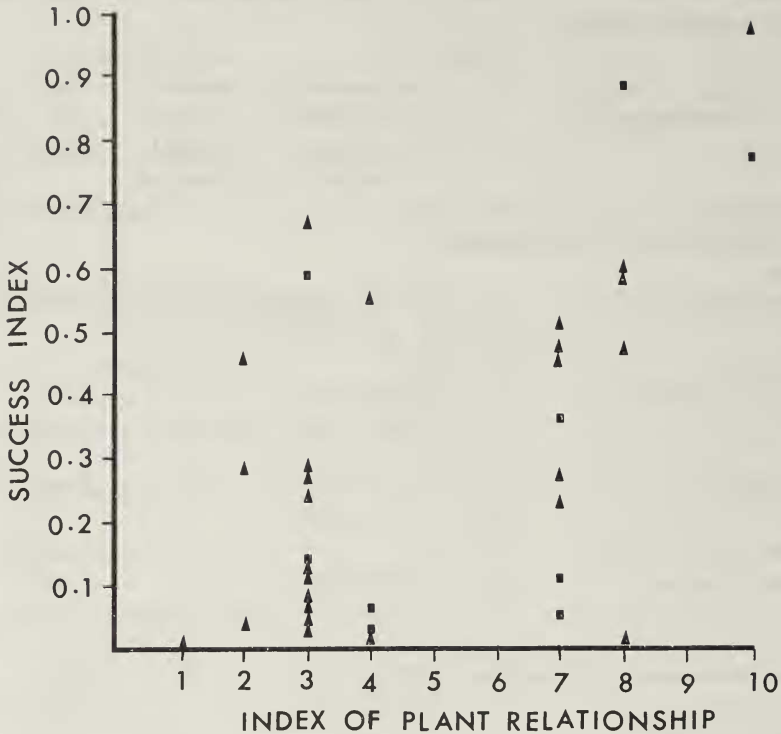
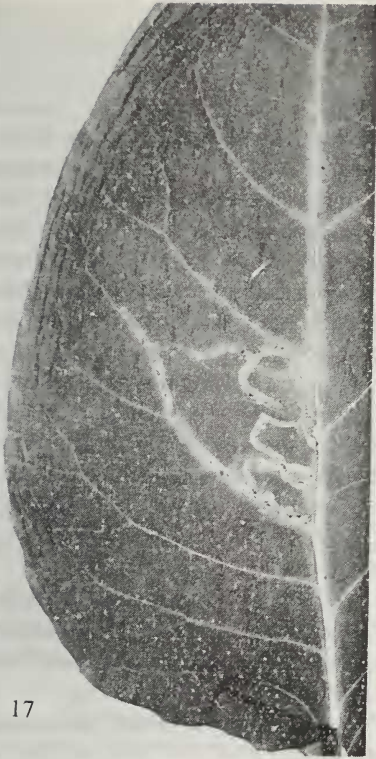


Fig. 16. Graph showing the success index of test plant for larval development against index of plant relationship. ▲ Transfers from *Tanacetum vulgare* L. ■ Transfers from *Achillea sibirica* Ledeb.

On the basis of available data, although it is not possible to make statistical comparisons of the relative success of larval development on these plants, nevertheless some of these plants were clearly more suitable for larval development than others. Two species outside the Compositae, *Pisum sativum* L. and *Galeopsis tetrahit* L., were at least as good as *Tanacetum*, their natural food plant, if not better, in their suitability for larval development. *Brassica* spp. tested were quite resistant to larval development; besides others, one reason was the formation of callus in the injured area of the young leaf. Among other plants tested, the formation of callus in the punctures made for feeding and oviposition, and in other small injuries, was very frequent in the young leaf of *Helianthus*.

Twelve dicotyledons were not used by larvae as food for complete development, though they did survive for a certain length of time in most of these plants. Among these plants the failure of larvae to mature in *Artemisia* sp. was probably due to the fact that they would bite their way out into the woolly fibres of the leaf. In all other plants the experimental larva died inside the tissue of the recipient plant.

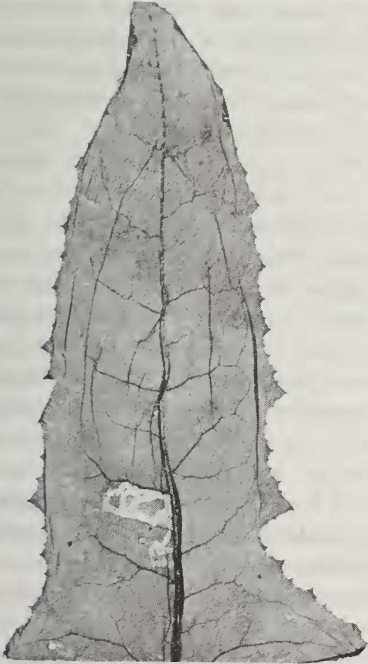
Among three monocotyledons, two species, *Allium cepa* L. and *Hordeum vulgare* L. were used by larvae to complete development to adult flies. The failure to use the third species *Typha latifolia* L. was, besides other factors, probably also due to the presence of large air spaces in the leaf tissue.



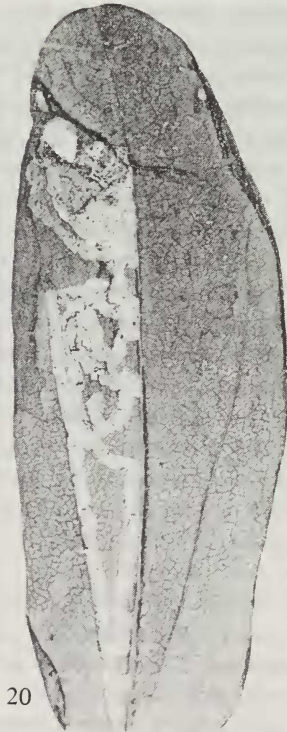
17



18



19



20

Fig. 17–20. Leaf mines formed after transfers of larvae of *Phytomyza matricariae* from *Tanacetum vulgare* to various recipient species. 17. leaf mine on *Brassica oleracea* L. 18. leaf mine on *Pisum sativum* L. 19. leaf mine on *Sonchus uliginosus* Bieb. 20. leaf mine on *Zinnia* sp. (cultivated).

DISCUSSION

Host-plant relationships of adult female

Range of food plants. — Even though females made varying numbers of feeding punctures on many plants, eggs were only deposited in members of the family Compositae belonging to the tribes Anthemideae and Heliantheae. Plants which are not accepted for both feeding and oviposition are considered as non-hosts. The physical characteristics of the plant do not seem to be important, although they may play some role in host preference. The acceptability of closely related plants for both feeding and oviposition indicate that chemical factors are involved in the very high degree of host-plant specialization. That many plants are not acceptable as hosts by *P. matricariae* is indicative of deterrent effects in the plants. Plants acceptable for feeding must therefore have stimulating substances and at the same time lack deterrent substances. Since the females oviposited only on closely related members of the family Compositae, the plants accepted for oviposition must also have substances which provide adequate stimuli for egg laying and these are not necessarily the same substances as those which stimulate feeding. Hsiao and Fraenkel (1968) working with Colorado potato beetle, *Leptinotarsa decemlineata* (Say), suggested that host specific stimuli from some solanaceous plants were required in the oviposition behavior of this species.

When the index of success in feeding and oviposition was compared with the index of plant relationship (Fig. 15), only plants most closely related to natural food plants were acceptable for feeding and oviposition, thus confirming the observed oligophagy of *P. matricariae* in nature.

Hering (1951) pointed out numerous species of mining insects in which the ovipositing females committed errors in their choice of host-plants and concluded that such instances of erroneous oviposition were quite common and yet escaped our attention. Later Nowakowski (1962) examined such known instances in the family Agromyzidae and found that these were mainly due to misidentifications of the insects. The results of the experiments on the host range of *P. matricariae* indicate that the females are unlikely to make the mistake of ovipositing on the wrong host under normal circumstances.

Feeding and oviposition preference of females. — When females were offered a choice of six acceptable plants for feeding and oviposition, *Tanacetum*, from which the flies used were obtained, was most preferred for feeding (Table 5); however, the numbers of eggs laid were not significantly higher than on some other plants in the test. In another experiment in which freshly emerged females obtained from pupae bred on *Tanacetum* were used, *Tanacetum* was still most preferred (Table 6) in number of feeding punctures. The preference for feeding on *Tanacetum* may either be explained by the preconditioning of the females in their own life, or by preconditioning in their larval life as defined by Hopkins' (1917) host selection principle, or by the greater quantity of substances which stimulate feeding, or just by the taste preference of the females. This however, cannot be clarified at present and would need further detailed studies. However, behavior in which insects prefer the plant species previously eaten is in agreement with the observations of Jermy, Hanson and Dethier (1968) on *Manduca sexta* (Johanssen) and *Heliothis zea* (Boddie). It may be pointed out that *Tanacetum* appeared to be more heavily attacked in nature than other host-plants. This, however, may also be due to various other factors like greater abundance of this plant in the habitat.

Among other plants used in the study *Achillea*, *Chrysanthemum*, and *Matricaria* were almost equally preferred, while *Helianthus* and *Artemisia* were least preferred for both feeding and oviposition (Tables 5, 6). The first three plants belong to the same tribe Anthemideae as *Tanacetum* and also serve as host-plants in nature. In *Chrysanthemum* only the

soft leaf variety was found to be attacked in nature. This suggests some importance of physical characteristics of plants in their selection. *Artemisia*, although closely related to *Tanacetum*, was not preferred, probably because the leaves used had a thick covering of woolly fibres on their lower surfaces, which may act as a physical barrier for females of this species. *Helianthus* which was also not preferred, is not as closely related to *Tanacetum*. It was also not found to be attacked in nature.

Hussey and Gurney (1962) suggested the use of feeding punctures to egg ratio as a method of assessing host preference in agromyzid species. The most 'preferred' host plant would have the lowest feeding puncture to egg ratio. They worked with a polyphagous species '*Phytomyza atricornis* Meigen' which was later shown by Griffiths (1967) to consist of two distinct species, *Phytomyza syngenesiae* (Hardy) feeding predominantly on composites and *Phytomyza horticola* Goureau feeding on composites and other families so that their results cannot be properly evaluated. In the populations used they found that feeding puncture to egg ratio was lower on preferred plants and concluded that preferred plants are nutritionally superior. It appears that the differential feeding and oviposition in their experiments with different varieties of *Chrysanthemum* was due to chemical factors which act as stimulants or deterrents rather than to nutritional differences.

Host-plant relationships of larvae

The ability of the larva to use 16 plants belonging to five different families for its development clearly shows that it is far less sensitive to deterrents than the adults which would only feed and oviposit on certain members of the family Compositae. The larvae having evolved a completely internal parasitic mode of life have reduced or poorly developed sense organs, which in turn reduces their ability to discriminate between various plant species. This is further supported by the observation that the larva starts feeding almost as soon as it is transferred to the test plant. The act of feeding was inferred from the movement of larval mouth hooks inside the test plant. However, the larva is capable of distinguishing between various kinds of tissue within the leaf, as only the mesenchymatous tissue is eaten. It is apparent that plants widely separated phylogenetically are nutritionally adequate for the completion of larval development, if they lack substances which are toxic or inhibitory.

Buhr (1937) was the first to carry out transplantation experiments with agromyzid larvae. He found that among the plants tested, the transferred larvae developed only on plants phylogenetically related to their natural food plant and died on plants not related to the normal host-plant. *Liriomyza eupatorii* (Kaltenbach) was exceptional, but it was already known to feed on *Eupatorium* (Compositae) and *Galeopsis* (Labiatae). He also succeeded in transferring larvae of *Liriomyza cannabidis* Hendel from *Cannabis* (Urticaceae), to *Eupatorium* and *Galeopsis*. However it is not known whether these two "species", *Liriomyza eupatorii* (Kaltenbach) and *L. cannabidis* Hendel, represent host races or sibling species, as was considered by Nowakowski (1962), since there is no clear morphological distinction between them.

Admittedly, the possibility that the agromyzid female would oviposit in nature on plants not closely related to the natural host-plant is very small. But, if the female did oviposit on plants outside the normal range, there is a good possibility that the larva would complete development, if the plant is not toxic or inhibitory. This is contrary to Nowakowski's (1962) suggestion that the probability of larval survival is very small.

This ability of the larvae to use successfully certain plants outside the range of normal host-plants of the ovipositing female in *P. matricariae*, can explain observed patterns in agromyzids and also in external feeders. *Liriomyza eupatorii* (Kaltenbach) normally feeds

in nature on *Eupatorium*, family Compositae and *Galeopsis*, family Labiatae. *Liriomyza brassicae* (Riley), an oligophagous species feeding on Cruciferae and related families, has also been reported to feed on *Pisum*, family Leguminosae (Spencer, 1964; Sehgal, 1965). Gupta and Thorsteinson (1960) showed that the leaves of non-cruciferous plants were normally accepted by the caterpillars of *Plutella maculipennis*, which normally feed on cruciferous plants. Jermy (1961) showed that Colorado potato beetle, normally a solanaceous feeder, accepted the leaves of *Asclepias syriaca* L., family Asclepiadaceae and *Allium cepa*, family Liliaceae. He later (1966) suggested that in these plants some other substances replace the specific phagostimulants. Hsiao and Fraenkel (1968) working on Colorado potato beetle found the leaves of *Asclepias* (Asclepiadaceae) and *Lactuca* (Compositae) to be the most suitable non-solanaceous plants and these plants could support reproduction and continuous culturing. They further reported that these plants were not fed upon in the presence of normal solanaceous hosts. They therefore concluded that host selection in this species was determined not only by the presence of adequate feeding stimuli and nutrients, but also by the presence of host specific substances which induce the initial feeding behavior. In *P. matricariae* such host specific substances could be important in the specificity of oviposition on certain members of the family Compositae, but not in the larval feeding on various test plants.

Jermy (1966) suggested that certain plants like *Pisum sativum* L. and *Malva sylvestris* L. seem to be in general free of strong feeding inhibitors, while others like *Solidago* are strongly deterrent. Results of transfers of larvae of *P. matricariae* support this view, as *Pisum sativum* was quite suitable for larval development while *Solidago* was not. *Galeopsis tetrahit* probably also belongs to a similar category of non-inhibitory plants.

The majority of species in the family Agromyzidae are restricted feeders, being monophagous or oligophagous (Sehgal, 1971). This study of insect host-plant relationships of adults and of larvae of *P. matricariae*, as well as recent studies involving other oligophagous species have shown that botanically unrelated plants can also serve as adequate food plants for normal development. However, in nature an oligophagous species normally selects botanically related plants for feeding and oviposition. Restricted feeding in nature on botanically related plant species or on unrelated plant species having similar secondary substances is probably the result of numerous evolutionary coadaptations of the phytophagous insect to the allelochemicals (Whittaker and Feeny, 1971), allomones and kairomones, of the host-plant(s).

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REFERENCES

- Ahmad, T. and R. L. Gupta. 1941. The pea leaf-miner, *Phytomyza atricornis* (Meigen), in India. Indian J. Ent. 3:37-49.
- Allen, P. 1956. Observations on the biology of some Agromyzidae (Diptera). Proc. R. ent. Soc. Lond. (A) 31:117-131.
- Allen, P. 1957. The larval morphology of Agromyzidae (Diptera). Proc. R. ent. Soc. Lond. (A) 32:59-66.
- Buhr, H. 1937. Parasitenbefall und Pflanzenverwandtschaft. Botan. Jahrb., 68:142-198.
- Cohen, M. 1936. The biology of the *Chrysanthemum* leaf-miner, *Phytomyza atricornis* Mg. (Diptera : Agromyzidae). Ann. appl. Biol. 23:612-632.
- Davis, P. H. and V. H. Heywood. 1965. Principles of Angiosperm Taxonomy. Oliver and Boyd. 558 pp.
- Dethier, V. G. 1966. Feeding behavior, *In* insect behavior. Symp. R. ent. Soc. London. 3:46-58.
- Dethier, V. G. 1970. Chemical interactions between plants and insects. *In* Chemical Ecology, E. Sondheimer and J. B. Simeone (eds.). Academic Press, New York. 83-102.
- Eames, A. J. 1961. Morphology of the Angiosperms. McGraw-Hill, New York.
- Fraenkel, G. S. 1959. The raison d'être of secondary plant substances. Science. 129:1466-70.
- Frick, K. E. 1952. A generic revision of the family Agromyzidae (Diptera) with a catalogue of New World species. Univ. Calif. Publs ent. 8:339-452.
- Friend, W. G. 1958. Nutritional requirements of phytophagous insects. Ann. Rev. Ent., 3:57-74.
- Griffiths, G. C. D. 1967. Revision of the *Phytomyza syngenesiae* group (Diptera: Agromyzidae), including species hitherto known as "*Phytomyza atricornis* Meigen". Stuttg. Beitr. Naturk. 177:1-28.
- Gupta, P. D. and A. J. Thorsteinson. 1960. Food plant relationships of the diamond-back moth [*Plutella maculipennis* (Curt.)] 1. Gustation and olfaction in relation to botanical specificity of the larva. Ent. exp. & appl. 3:241-250.
- Harris, P. and A. I. Mohyuddin. 1965. The bioassay of insect feeding tokens. Can. Ent. 97:830-833.
- Hering, E. M. 1951. Biology of the leaf miners, 's-Gravenhage: 1-420.
- Hering, E. M. 1957. Bestimmungstabellen der Blattminen von Europa. 's-Gravenhage, 3 vol., I: 1-648, II: 649-1185, III: 1-221.
- Hopkins, A. D. 1917. A discussion of C. G. Hewitt's paper on "Insect Behavior". J. econ. Ent. 10:92-93.
- Hsiao, T. H. and G. Fraenkel. 1968. Selection and specificity of the Colorado potato beetle for solanaceous and nonsolanaceous plants. Ann. ent. Soc. Amer. 61:493-503.
- Hussey, N. W. and Gurney, B. 1962. Host selection by the polyphagous species *Phytomyza atricornis* Meigen (Dipt., Agromyzidae). Entomologist's mon. Mag. 98:42-47.
- Hutchinson, J. 1964. The families of flowering plants. Oxford University Press.
- Jermey, T. 1961. On the nature of the oligophagy in *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae). Acta Zool. Acad. Sci. Hung. 7:119-132.
- Jermey, T. 1964. The role of rejective stimuli in the host selection of phytophagous insects. Proc. XII Int. Congr. Ent. London. 1964 (1965) p. 547.
- Jermey, T. 1966. Feeding inhibitors and food preference in chewing phytophagous insects. Ent. exp. & appl. 9:1-12.
- Jermey, T., F. E. Hanson and V. G. Dethier. 1968. Induction of specific food preference in Lepidopterous larvae. Ent. exp. & appl. 11:211-230.

- Keller, J. C. and T. B. Davich. 1965. Response of five species of insects to water extracts of their host plants. *J. econ. Ent.* 58:164.
- Kennedy, J. S. 1965. Mechanisms of host plant selection. *Ann. appl. Biol.*, 56:317-22.
- Lipke, H. and G. Fraenkel. 1956. Insect nutrition. *Ann. Rev. Ent.* 1:17-44.
- Meijere, J. C. H. de. 1926. Die Larven der Agromyziden. *Tijdschr. Ent.* 69:227-317.
- Nayar, J. K. and G. Fraenkel. 1962. The chemical basis of host plant selection in the silk-worm *Bombyx mori* L. *J. Insect. Physiol.* 8:505-525.
- Nayar, J. K. and G. Fraenkel. 1963. The chemical basis of host selection in Mexican bean beetle *Epilachna verivestis* (Muls). *Ann. ent. Soc. Amer.* 56:174-178.
- Nowakowski, J. T. 1962. Introduction to a systematic revision of the family Agromyzidae (Diptera) with some remarks on host-plant selection by these flies. *Ann. zool., Warszawa* 20(8):67-183.
- Nowakowski, J. T. 1964. Studien über Minierfliegen (Dipt. Agromyzidae) 9. Revision der Artengruppe *Agromyza reptans* Fall. — *A. rufipes* Meig. *Dt. Ent. Z. (N.F.)* 11:175-213.
- Oatman, E. R. and A. E. Michelbacher. 1958. The melon leaf miner, *Liriomyza pictella* (Thomson) (Diptera: Agromyzidae). *Ann. ent. Soc. Amer.* 51:557-566.
- Oatman, E. R. and A. E. Michelbacher. 1959. The melon leaf miner, *Liriomyza pictella* (Thomson) (Diptera: Agromyzidae). *Ann. ent. Soc. Amer.* 52:83-89.
- Schoonhoven, L. M. 1968. Chemosensory bases of host plant selection. *Ann. Rev. Ent.* 13:115-136.
- Sehgal, V. K. 1965. Studies on Indian Agromyzidae (Diptera). *Beitr. Ent.* 15:3-10.
- Sehgal, V. K. 1971. (in press). A taxonomic survey of the Agromyzidae (Diptera) of Alberta, Canada, with observations on host-plant relationships. *Quaest. ent.*
- Smulyan, M. T. 1914. The Marguerite fly or *Chrysanthemum* leaf miner. *Bull. Mass. agr. Exp. Sta. No.* 157:21-52.
- Spencer, K. A. 1964. The species-host relationship in the Agromyzidae (Diptera) as an aid to Taxonomy. *Proc. 12th int. Congr. Ent. (London 1964)* 1:101.
- Spencer, K. A. 1969. The Agromyzidae of Canada and Alaska. *Mem. ent. Soc. Can.*, 64: 311 pp.
- Stride, G. O. 1965. Studies on the chemical basis of host-plant selection in the genus *Epilachna* (Coleoptera, Coccinellidea). *J. Insect Physiol.*, 1965:21-32.
- Sugiyama, S. and Y. Matsumoto. 1959. Olfactory responses of the vegetable weevil larvae to various mustard oils. *Nōgakū kenkyū* 46:150-157.
- Takhtajan, A. 1969. Flowering plants, origin and dispersal, Oliver and Boyd, 205-239 pp.
- Tauber, J. M. and C. A. Tauber. 1968. Biology and leaf-mining behaviour of *Phytomyza lanati* (Diptera: Agromyzidae). *Can. Ent.* 100:341-357.
- Thorsteinson, A. J. 1953. The chemotactic basis of host plant selection in an oligophagous insect. (*Plutella maculipennis* Curt.). *Can. J. Zool.* 31:52-72.
- Thorsteinson, A. J. 1960. Host selection in phytophagous insects. *Ann. Rev. Ent.* 5:193-218.
- Tilden, J. S. 1950. Oviposition and behavior of *Liriomyza pusilla* (Meigen) (Diptera: Agromyzidae). *Pan-Pacif. Ent.*, 26:119-121.
- Trehan, K. N. and V. K. Sehgal. 1963. Range of host plants and larval feeding in *Phytomyza atricornis* (Meigen) (Dipt., Agromyzidae). *Ent. mon. Mag.* 99:1-3.
- Verschaffelt, E. 1910. The cause determining the selection of food in some herbivorous insects. *Proc. Acad. Sci. Amsterdam* 13:536-42.
- Webster, F. M. and T. H. Parks. 1913. The serpentine leaf-miner. *J. Agric. Res.* 1:59-87.
- Whittaker, R. H. and P. P. Feeny. 1971. Allelochemicals: chemical interactions between species. *Science*. 171, No. 3973:757-770.